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Soil solarization based on natural soil moisture: a practical approach for reducing the seed bank of invasive plants in wetlands

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Abstract

Soil solarization is a well-established method to disinfect soil for efficient weed control. However, the feasibility of applying this method in the restoration of invaded natural habitats is unclear. This is because soil moisture is necessary for the success of solarization, but pre-irrigation in natural ecosystems is often not applicable, or demands high labor investment, making it unsuitable for use in restoration. The present study was based on the idea that the relatively high soil moisture in wetlands might obviate the need for pre-irrigation, rendering this method much more applicable in natural habitats. We examined the efficacy of soil solarization using natural soil moisture to control the seed bank of the invasive plant, *Acacia saligna,* in a wetland, using large-scale experimental plots (0.38 ha each). An old, dense *A. saligna* grove was cut down and the roots were removed by a bulldozer. The plot was mulched with a transparent polyethylene sheet in early July and left on the soil for 14 weeks. Soil solarization significantly reduced the viability of seeds of *A. saligna* that had been experimentally buried. Additionally, viability of seeds in the natural seed bank was reduced, and seedling emergence was close to zero. Exposing seeds to soil temperature and soil moisture levels equivalent to those obtained during field soil solarization under controlled conditions significantly increased the release from dormancy of the seeds, suggesting that release from dormancy during the early stage of solarization is a critical stage leading to seed weakening or mortality in the soil. Soil solarization also decreased the cover and abundance of the natural vegetation; therefore, active revegetation is required to restore the natural vegetation and to conserve endangered and endemic species.

Keywords
Acacia saligna, invasive plant control, physical dormancy, restoration, soil disinfestation, seed dynamics

Introduction

The world has lost 87% of its wetlands since 1700 AD (Davidson 2014). In recent decades, the loss and degradation of the wetlands has accelerated due to anthropogenic factors, including the proliferation of invasive species. It is well known that wetlands are especially vulnerable to plant invasion (Zedler and Kercher 2004) . The re-establishment of invasive plants from long-term persistent soil seed banks is one of the most important factors leading to the failure of restoration efforts (Zavaleta et al. 2001; Erskine Ogden and Rejmánek 2005; Reid et al. 2009; Le Maitre et al. 2011).

Attempts to control the seed banks of invasive plants having physically dormant seeds in natural habitats have been based mainly on the use of prescribed burning (Richardson and Kluge 2008). However, unsatisfactory results and the limitations of using prescribed burning in many natural habitats have led to efforts to develop new efficient control methods. Recently, for example, microwave soil heating has been suggested as a potential method to control the seed bank of invasive plants in natural habitats (De Wilde et al. 2017; Hess et al. 2018), but an applicable device has not yet been developed. Our group, using *Acacia saligna* as a model plant, demonstrated that soil solarization has high potential as a control method for this purpose in natural habitats undergoing restoration.

Soil solarization is a well-established soil disinfestation practice in agriculture. It is used as a pre-planting treatment, and was originally designed to reduce populations of pests, pathogens, and weeds. Soil solarization consists of mulching a moist soil with transparent polyethylene sheets during the hot season. The trapped solar radiation warms the soil and transfers the heat generated to the deep soil layers. Hence, soil temperatures are raised to lethal or sub-lethal levels for a wide spectrum of soil organisms (Horowitz et al. 1983; Gamliel 2012; Bainbridge 2016). Soil moisture, which is usually acquired by irrigation, is necessary for heat penetration into the deep soil layers and to increase the sensitivity of organisms to the thermal effect. With respect to weed seeds, soil solarization can induce seed bank deterioration through three processes: 1. breaking dormancy which results in seed germination; 2. seed mortality; 3. weakening effect, i.e reduced seed vigor which results in non-normal germination and vulnerability to biotic stresses (Katan 2003; Cohen and Rubin 2007).

In recent years, our group has been working on adapting the soil solarization methods commonly used in agriculture for the restoration of invaded natural habitats. The model plant which has been used in our studies is *A. saligna* (Labill.) Wendel. F. (Port Jackson Willow), a small legume tree belonging to the invasive Australian *Acacia* group (Le Maitre et al. 2011). This species has been planted at a wide scale (about 600,000 ha) outside of Australia and has become a serious invader in various countries worldwide characterized by a Mediterranean climate (Griffin et al. 2011). *Acacia saligna* produces thousands of physically dormant seeds per square meter yearly that accumulate

into an exceptionally long-lived, persistent seed bank (Milton and Hall 1981; Holmes and Newton 2004). Cohen et al. (2008) first applied the soil solarization method to control woody *Acacia* species in an experimental farm and showed that the solarization treatment resulted in almost complete eradication of buried seeds of *A. saligna* and two other Australian *Acacia* species, *A. murrayana* F.Muell. ex Benth. and *A. sclerosperma* F.Muell. Recently, Cohen et al. (2018) reported that soil solarization was more effective than prescribed burning in reducing the viability of buried seeds of *A. saligna* in a Mediterranean coastal plain and almost completely reduced its seedling emergence from the natural seed bank during two successive years after treatment. Pre-irrigation in natural ecosystems is often not applicable or demands high labor investment, rendering soil solarization unsuitable for use in restoration programs. Therefore, attempts have been made to develop methods which will eliminate the need for irrigation. Cohen et al. (2019) recently reported the successful application of rain-based solarization to control the seed bank of *A. saligna*. This method is based on trapping the soil moisture caused by the last rainfall in the early spring. The data obtained demonstrated a significant reduction of *A. saligna* seed bank in both Mediterranean and semi-arid climates and in different soil types. This treatment also completely reduced the seed viability of three other invasive legumes that were buried in the experimental site, *A. victoriae* Benth., *Parkinsonia aculeata* L., and *Leucaena leucocephala* (Lam.) de Wit. Our previous studies demonstrated that moderate soil moisture can effectively reduce the seed bank of *A. saligna* at the moderate soil temperatures created by soil solarization (Cohen et al. 2019).

The objective of the present study was to assess the effectiveness of dry-soil solarization (hereafter, called simply solarization) on reducing the seed bank of *A. saligna*. This solarization entailed covering the soil with transparent polyethylene sheets during the hot summer season without pre-irrigation. It is well accepted that in wetlands, the high water table contributes to increased soil moisture in the overlying soil layers (Miguez-Macho et al. 2008 and literature cited therein). Under these conditions, the evaporated soil moisture condenses on the polyethylene sheet, drips back onto the soil surface, and rewets it (Al-Karaghouli and Al-Kayssi 2001). Thus, in wetlands, solarization might raise both temperature and moisture in the upper soil layer above the threshold levels required for release from dormancy, thereby accelerating seed bank deterioration.

Methods

Experimental site

The experimental site is located in the Samach Estuary on the eastern bank of the Sea of Galilee (Lake Kinneret, 32°50'03"N, 38°35'57"E). The climate is semi-arid (264 mm average annual precipitation). The experiment was conducted at about 500 m from the shoreline. The soil is alluvial, comprising 46% sand, 34% silt, and 20% clay. The experiment was initiated in early July and lasted for 14 weeks. This period is regarded as the most effective solarization period in the Mediterranean region. According to the

Beit Saida meteorological station, the average maximum daily air temperature during this period was 35.4 °C. The local natural vegetation outside the *A. saligna* stand in this habitat is dominated by species such as *Prosopis farcta* (Banks & Sol.) J.F.Macbr and *Glycyrrhiza glabra* L., which extend along the margins of irrigated fields. These species naturally occupy the wetland edges in Israel. The experiment was set up in an established *A. saligna* grove, which was planted in 1972. From the original planted groove, *A. saligna* trees have spread to the surrounding habitats (~19.3 ha), both in disturbed and undisturbed areas, and previous attempts to control the invasive trees have failed. The canopy cover of the trees in the experimental site was very high (80–100% shade).

Preliminary measurements

Prior to the initiation of the experiment, the seed bank density of *A. saligna* and vegetation cover were evaluated along two transects running along the length and width of the area under the *A. saligna* canopies. Eight soil cores, 7.2 cm in diameter and 20 cm long, were sampled along each transect by means of a metal pipe. The average seed density was 132.1 ± 54.6 seeds/L, with no significant differences among sites along the two transects. Vegetation charts were made in eight plots (10 m × 10 m, about 50 m apart from each other) along the two transects mentioned above. Vegetation cover and composition under the *A. saligna* canopy were homogenous. Excluding *A. saligna* seedlings, the vegetation cover in the plots constituted 1–20% of the area under the *A. saligna* tree canopies. This vegetation included a total of 15 plant species, dominated by the nitrophilic species, *Notobasis syriaca* (L.) Cass., *Mercurialis annua* L., and *Torillis arvensis* (Huds.) Link.

Experimental design

As no significant changes in *A. saligna* seed bank density and vegetation cover and composition were evident along the two transects under the *A. saligna* canopy, the experimental area was divided along its length into two treatments, control (non-solarized bare soil) and solarization. Each treatment was conducted in a large plot of 0.38 ha. Large plot size has the benefit of simulating the practical application of the treatment.

All *A. saligna* trees in the grove were cut down in November 2014, piled, and burned. Glyphosate (Rodeo, 53.8% active ingredient, Dow Chemical Company, MI, USA) at a concentration of 50% was applied to the surface of the remaining stumps. In June 2015, the tree stumps were uprooted with a D9 bulldozer root rake (50-cm teeth), and the soil was leveled. On July 1, 2015, the solarization plot was mulched with a transparent polyethylene sheet (anti-fog 100 μm, Politiv, Kibbutz Einat, Israel). The parameters measured during the experiment included soil moisture, soil temperature, dynamics of buried seeds, i.e. transition from dormant seed fraction to non-dormant or non-viable seed fractions, density of the *A. saligna* seed bank and seedling emergence from the seed bank, and the density, growth, and composition of the regenerated vegetation.

Soil moisture and soil temperature

Soil moisture was monitored during the experiment in soil samples taken at 6, 28, 43, 51, and 66 days after mulching. At each sampling date, four soil cores, 7.2 cm in diameter and 20 cm long, were sampled from random locations in each treatment, at 20-m spacing, by means of a core auger. Each soil sample was divided into two subsamples representing two different depths: 0–5 cm (shallow layer) and 15–20 cm (deep layer). Samples of 250 ml soil were taken from each subsample, and weighed before and after drying at 105 °C for 24 h. Soil moisture was calculated as a percentage of the sample dry weight.

Soil temperature in the control and solarization plots was continuously recorded at depths of 5, 10, 15, and 20 cm, using a type T thermocouple connected to a micrologger (10×, Campbell Scientific Inc. Logan, UT). Air temperature was recorded with a portable meteorological station positioned in the shade at the edge of the solarization plot, 0.5 m above ground level.

Evaluation of buried seed dynamics

Acacia saligna seeds were collected in mid-June from 10 trees within a radius of 2 km from the study site. The viability of the collected seeds was 100%, and 96.7% of them were dormant. The seeds were placed in nylon net bags, 30 seeds in each bag (Cohen et al. 2008). Four seed bags were tied separately to a nylon string and buried in the soil so that each bag was buried at a different soil depth: 1–4, 6–9, 11–14, and 16–19 cm. Sixteen such strings were buried in each treatment plot. Four strings with seed bags were removed from the soil at 31, 43, 52, and 72 days after mulching. The seed dynamics was determined in the laboratory by two successive germination tests. The first test was conducted on intact seeds and the second was conducted after scarification of the seed coat. The seeds were placed between moist filter papers for 20 days in the first germination test and for 10 days in the second germination test. Seeds were considered germinated when the primary root was longer than 2 mm. Seed dynamics were classified into the following categories: 1. seeds that germinated in the first test were defined as non-dormant; 2. seeds that germinated only in the second test were defined as dormant; 3. seeds that did not germinate in either germination test were defined as non-viable.

Acacia saligna natural seed bank density and seedling emergence

The effect of solarization on the density of the *A. saligna* seed bank and seedling emergence from the seed bank was examined in the first spring (March) after treatment, We observed that *A. saligna* seeds are concentrated in the upper 5 cm soil layer, even after deep tillage (data not shown). Therefore, 16 soil cores in each treatment were sampled up to 5 cm depth from random locations at about 20 m spacing using a core

auger as described above. The soil cores were sampled in March (spring), when the soil was moist. Emerging seedlings were counted in the soil samples, then the soil was sieved, and the seeds obtained were tested for viability as described above. The density of the viable seeds in the soil was calculated as number per liter of soil. The density of emerged seedlings was calculated as number per square meter.

Natural vegetation cover

The effect of solarization on the regeneration of the natural vegetation was evaluated by constructing vegetation charts in the first spring after treatment in four sites of 100 m^2 in each treatment. The charts included the relative cover of each plant species per area, as well as the following revegetation parameters: vegetation cover per area (%), number of species, vegetation height, and Shannon diversity index (i).

Effect of soil temperature and soil moisture on *A. saligna* seed dynamics under controlled conditions

Thirty *A. saligna* seeds were placed in glass tubes containing dry sand pre-heated to 105 °C for 24 hours and adjusted to 5 or 11% water content. The tubes were sealed and incubated in a water bath at 24, 48, and 57 °C for 72 hours. The selected exposure temperatures comply with those recorded in the field experiment in the solarization treatment (Fig. 2). The effect of the treatments on the seed dynamics (dormant, non-dormant, and non-viable fractions) was examined using the germination tests as described above. The experimental design was fully factorial and included five replicates, 30 seeds in each.

Statistics

The JMP 13 statistical package was used for data analysis. A Levene's test ($P = 0.05$) for equality of variances was used for the soil moisture data. Percentage values were transformed to log. A three-way ANOVA ($P = 0.05$) was used to examine the effect of treatment, depth, experimental duration, and their interactions on soil moisture, followed by post-hoc t-test ($P = 0.05$) for means comparisons between treatments. Buried seed data were analyzed by three-way ANOVA ($P = 0.05$) to examine the effect of treatment, soil depth, experimental duration, and their interactions. The ANOVA was followed by post-hoc t-test ($P = 0.05$) for means comparisons between treatments or Tukey's test ($P = 0.05$) for means comparisons between all main effects and their interactions. In situations of interaction between treatment, soil depth, and duration, the data from the solarization treatment were compared to the control under each set of conditions (soil depth and duration) using a preplanned contrast t-test ($P = 0.05$). All percentage values of the various seed fractions were transformed to arcsine. Seed bank density was analyzed using t-tests

($P = 0.05$) for means comparisons between treatments or Tukey's test ($P = 0.05$) for means comparisons between soil depths within a treatment. The depth of seedling emergence was analyzed by contrast *t*-tests ($P = 0.05$). All the revegetation parameters – relative cover, vegetation height, species richness, and Shannon diversity index (H') – were also analyzed by *t*-tests ($P = 0.05$). The laboratory data on the effect of temperature and soil moisture on the buried seed fractions were analyzed by a two-way ANOVA ($P = 0.05$), followed by a post-hoc Tukey's test ($P = 0.05$) for means comparisons between treatment combinations.

Results

Effect of solarization on soil moisture and soil temperature

Soil water moisture in the solarization treatment was 5.4%, significantly higher ($t = 5.6941$, $P < 0.0001$) than that in the control (3.1%, Fig. 1.). It should be noted that the soil moisture varied greatly between measurements in the solarization treatment. Based on three-way ANOVA (Suppl. material 1: Table S1), solarization appears to be the only significant factor affecting soil moisture ($F_{1,6} = 10.63$, $P < 0.017$).

The maximum daily temperature in the solarization treatment at soil depths of 1, 5, 10, and 20 cm was 64.3, 57.6, 49.8, and 42.6 °C, respectively, compared with 58.2, 48.9, 41.8, and 36.4 °C, respectively, in the control (Fig. 2). The minimum daily temperature in the solarization treatment at depths of 1, 5, 10, and 20 cm was 28.7, 32.1, 35.5, and 37.9 °C, respectively, and in the control, 23.8, 27.5, 30.4, and 32.7 °C, respectively. While at 1 cm depth, the soil temperature during the day in the control exceeded 55 °C for 2 to 3 h, in the solarization treatment these conditions continued for 5–6 h. At this depth, soil temperature exceeded 60 °C only in the solarization treatment, for 3–4 h a day.

Effect of solarization on buried seed dynamics

The effect of solarization on buried seed dynamics, i.e. the dormant, non-dormant, and non-viable fractions, at four soil depths was studied on four dates during the 16-week experimental duration (Fig. 3). Solarization significantly reduced the dormant seed fraction in all measurements to 22.0% from 63.3% observed in the control (*t*-test, $P < 0.0001$). However, while the dormant fraction in the control did not change significantly with soil depth (Tukey's-test, $P < 0.005$), the effect of solarization on the release from seed dormancy decreased significantly with increasing soil depth, the dormant fraction being 8.3% at 1–4 cm compared to 42.9% at 11–16 cm soil depth. According to the three-way ANOVA analysis (Suppl. material 2: Tables S2, S3a), the dormant seed fraction was affected by both treatment ($F_{1,25} = 121$, $P < 0.0001$) and depth ($F_{3,73} = 8.46$, $P < 0.0001$) and by their interaction ($F_{3,73} = 9.82$, $P < 0.0001$). The experimental duration did not affect the dormant seed fraction, either as a main factor or in interaction with the other factors.

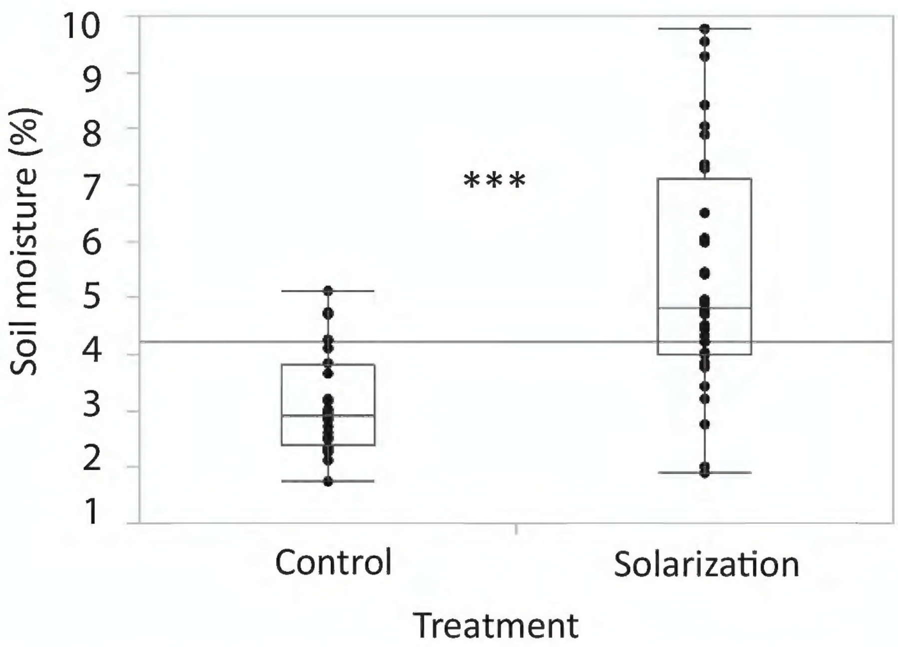

Figure 1. Comparison of the soil moisture between the control and the solarization treatment. Soil measurements were performed at 0–5 and 15–20 cm soil depths on four dates (4, 6, 11, and 14 weeks) after initiation of the treatment. The box-plot for each treatment includes the median, quartile, minimum, and maximum values. Points represent observations; n = four replicates × two soil depths × four experimental durations, *** = $P < 0.0001$ according to a post-hoc t-test (0.05) following three-way ANOVA (see Suppl. material 1: Table S1).

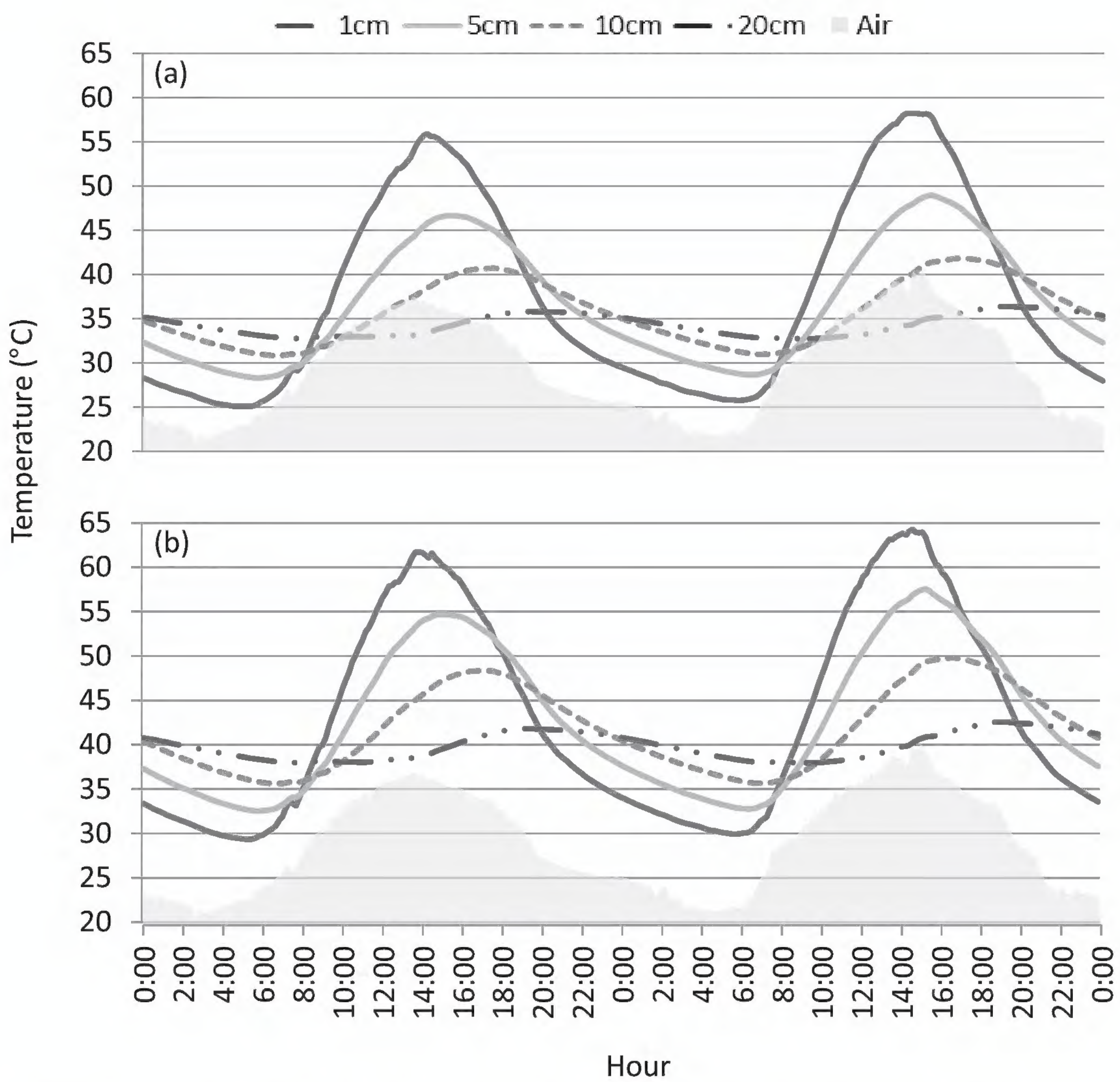

Figure 2. Comparison of soil temperature fluctuations in the control (**a**) and the solarization treatment (**b**) The temperature was measured at four soil depths (1, 5, 10, and 20 cm). The data represent the soil temperature during two successive days in mid-July. Air temperature is represented by the gray polygon in each figure.

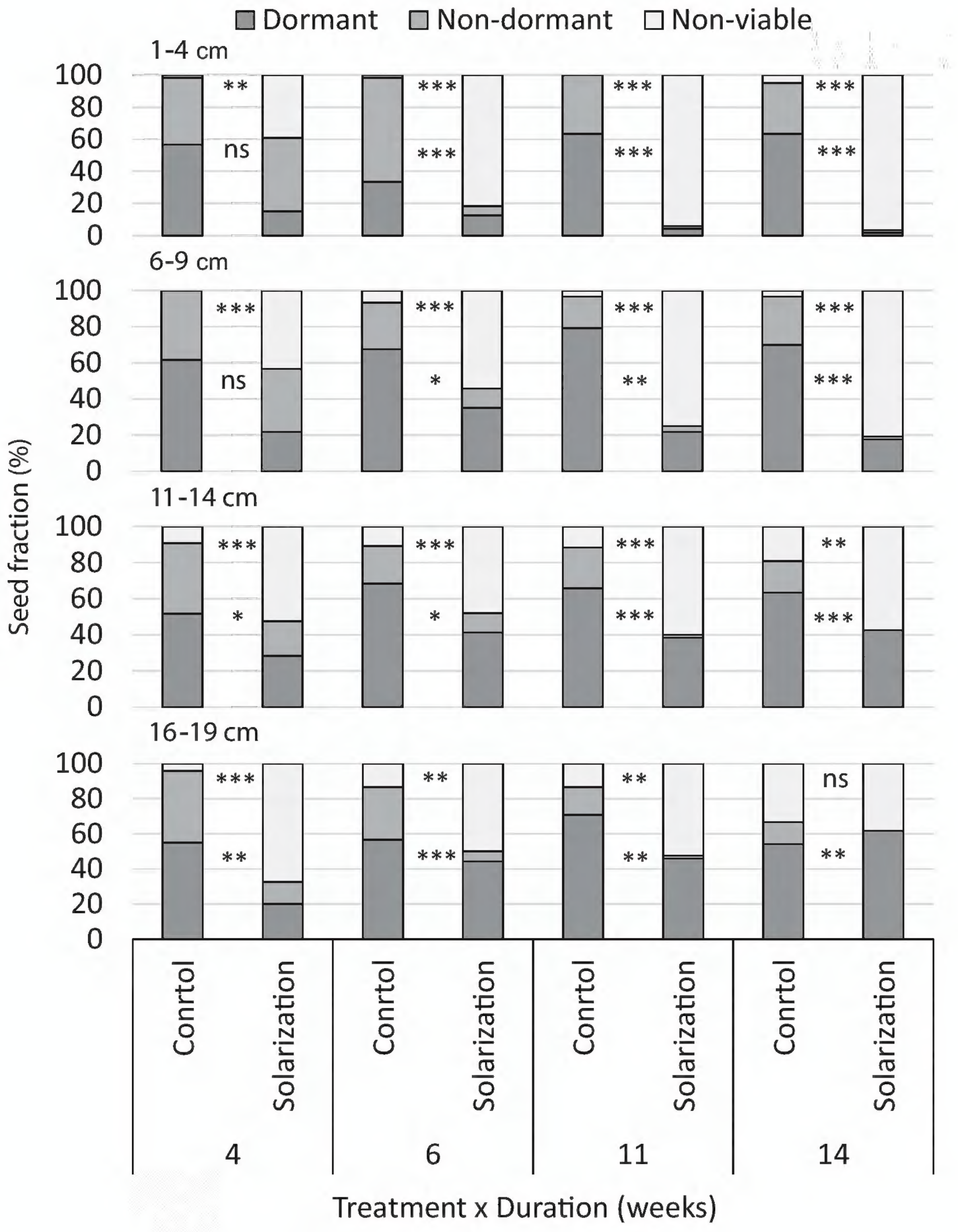

Figure 3. Comparison of *Acacia saligna* buried seed dynamics (dormant, non-dormant, and non-viable fractions) in the control and the solarization treatment. The data were collected in 16 combinations of soil depth and experimental duration. Significance levels (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$) of a priori means comparison *t*-tests ($P = 0.05$) are presented for the non-viable and the non-dormant fractions. The dormant fraction was not significantly affected by the interaction of treatment, soil depth, and experimental duration. *n* = four seed bags for each combination, 30 seeds in each.

Solarization significantly increased the non-dormant seed fraction during the experimental period at all soil depths compared to the control (Fig. 3). In both the control and the solarization treatment, the non-dormant seed fraction decreased significantly with the increase of the experimental duration, from 40.0 to 22.1% in the control and from 28.1 to 0.8% in the solarization treatment after 4 and 14 weeks, respectively. According to the three-way ANOVA analysis (Suppl. material 2: Tables S2, S3b), the non-dormant seed fraction was significantly affected by treatment ($F_{1,25} = 92.25$, $P < 0.0001$), soil depth ($F_{3,73} = 7.95$, $P < 0.0001$), experimental duration ($F_{3,25} = 22.6$, $P < 0.0001$), the interaction between treatment and duration ($F_{3,25} = 3.79$, $P < 0.0001$), and the interaction between treatment, depth, and duration ($F_{9,73} = 2.59$, $P = 0.012$).

The solarization treatment significantly increased the non-viable fraction above that measured in the control, excluding the fraction at 16–19 cm after 14 weeks (Fig. 3). In addition, while the results of Tukey's test (P = 0.05) show that the non-viable seed fraction in the control did not vary with soil depth or experimental duration, these factors had a significant effect on this fraction in the solarization treatment: the non-viable fraction decreased significantly with soil depth and increased with the increase in the experimental duration only in the upper 9 cm of the soil profile. According to the three-way ANOVA (Suppl. material 2: Tables S2, S3c), the non-viable seed fraction (i.e. seed mortality) was affected by treatment ($F_{1,25}$ = 220.2, P < 0.0001), the interaction between treatment and soil depth ($F_{3,72}$ = 14.05, P < 0.0001), experimental duration ($F_{3,25}$ = 3.80, P < 0.0228), and the interaction between treatment, soil depth, and experimental duration ($F_{9,72}$ = 4.63, P < 0.001).

Effect of solarization on *A. saligna* seed bank and seedling emergence

Solarization significantly reduced the density of the *A. saligna* seed bank (t = 5.4, P < 0.0001, Fig. 4a) and completely eliminated seedling emergence from the seed bank (Figs 4b, 5). It should be noted that seedling emergence in the control was closed to 1,000 seedlings per square meter.

Effect of solarization on the regeneration of the natural vegetation

Solarization significantly decreased the regenerated vegetation cover per area compared to the control (Fig. 6a, t = 39.432, P < 0.0001). Similar results were obtained for the vegetation height (Fig. 6b, t = 5.125, P = 0.0143). The species number (Fig. 6c) and the Shannon diversity index (Fig. 6d) did not differ significantly between treatments.

Effect of soil temperature and soil moisture on *A. saligna* seed dynamics under controlled conditions

The viable seed fraction exceeded 96% in all the six treatment combinations of soil temperature and moisture (Fig. 7). There was a strong expression of release from dormancy, i.e. a decrease in the dormant seed fraction, and a concurrent increase in the non-dormant fraction with the increase in soil temperature and soil moisture. The dormant seed fraction decreased significantly with the increase in soil temperature and soil moisture from 89.8% at 24 °C and 5% moisture to 35.4% at 56 °C and 11% moisture. The results of the two-way ANOVA show that the dormant fraction was significantly affected by soil temperature ($F_{2,0.5}$ = 84.61, P < 0.0001), soil moisture ($F_{1,0.05}$ = 16.08, P = 0.0005), and the interaction between them ($F_{21,0.04}$ = 7.02, P = 0.0042).

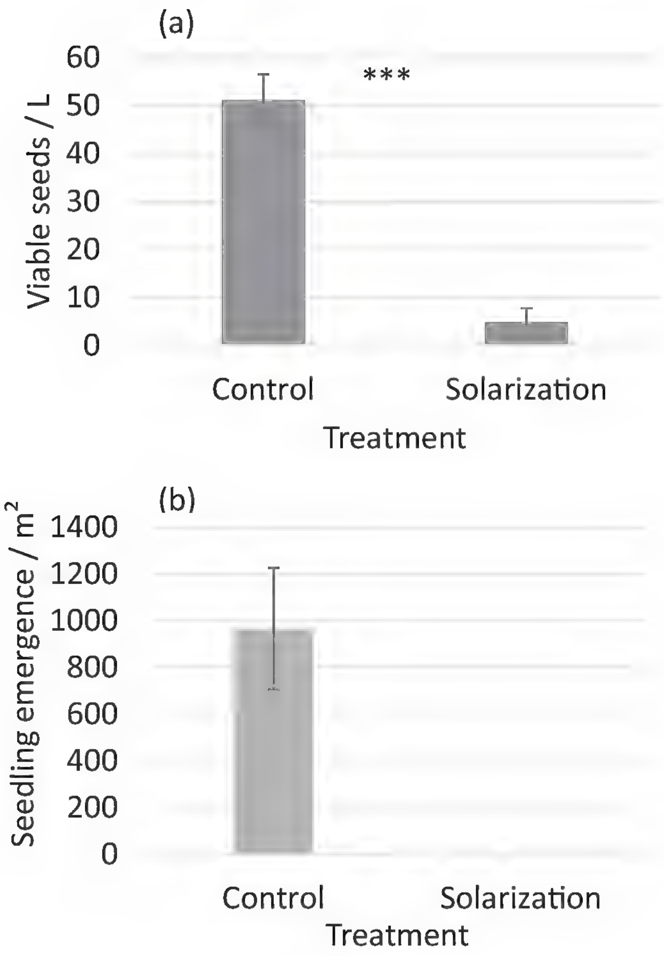

Figure 4. Comparison of *Acacia saligna* seed bank density (**a**) and seedling emergence from the seed bank (**b**) in the control and the solarization treatment. The samples were taken in the first spring (March) after treatment. Means of either seed number per liter of soil or seedling emergence per m^2 represent 16 samples (replicates) of 0–5 cm soil depth. Significance levels *** = $P < 0.001$ according to a contrast *t*-test.

Figure 5. Demonstration of the efficacy of solarization in controlling *Acacia saligna* seedling emergence and vegetative sprouting. The picture was taken in the first winter after treatment (mid-February). The solarization plot is almost completely void of vegetation. Vegetation cover in the control plot includes almost one thousand *A. saligna* seedlings per m^2, *A. saligna* vegetative sprouts, and other nitrophilic plants that are common in revegetated areas following *A. saligna* removal, including Brassicaceae, Compositae, and Malvaceae species.

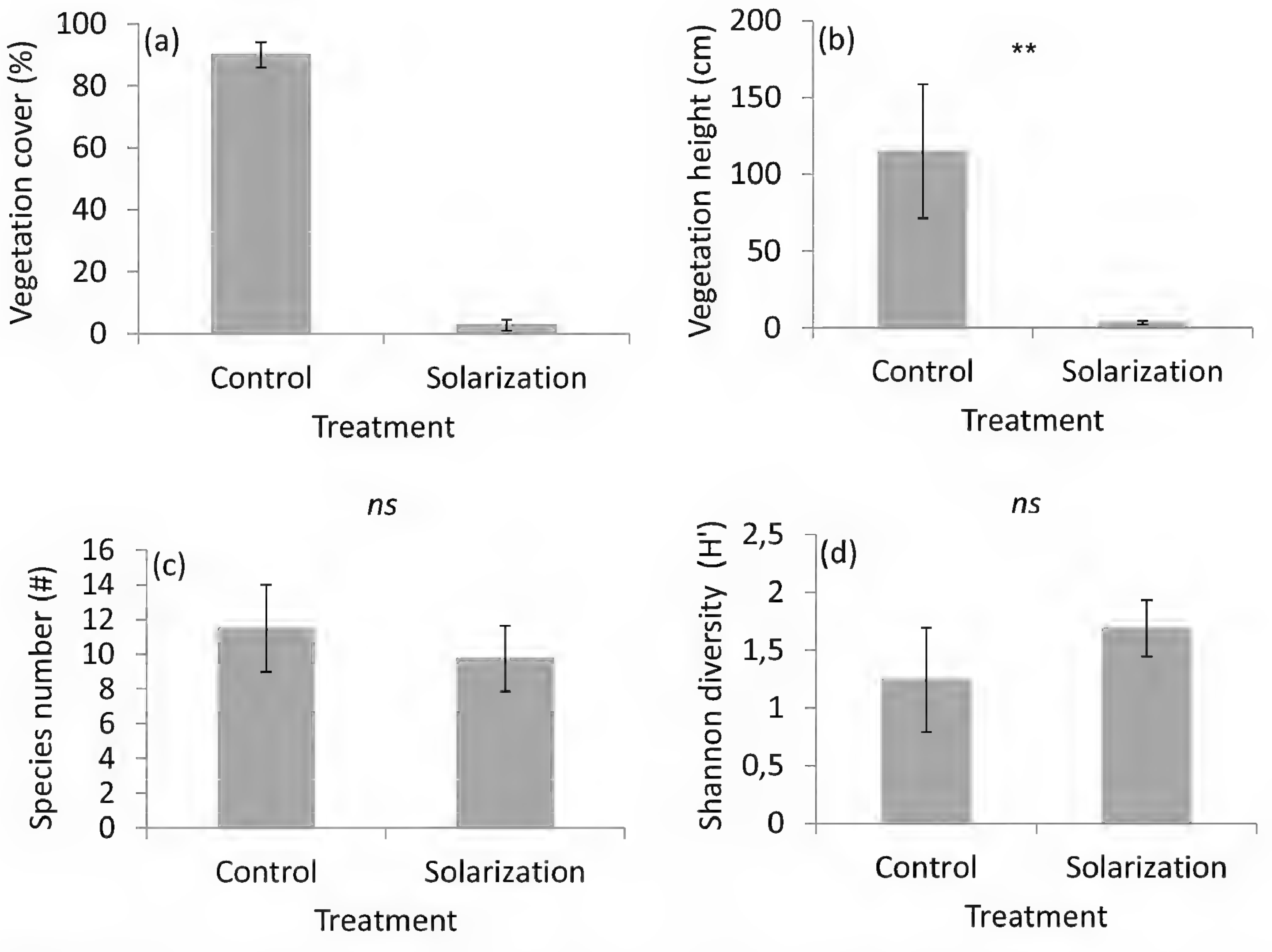

Figure 6. Comparison of the vegetative regeneration in the control and the solarization treatment. The vegetation parameters were measured in the first spring after treatment in four sites of 100 m^2 in each treatment. The parameters measured were vegetation cover (**a**), vegetation height (**b**), number of species (**c**), Shannon diversity (H') (**d**). *n* = four replicate plots, each 10 × 10 m.

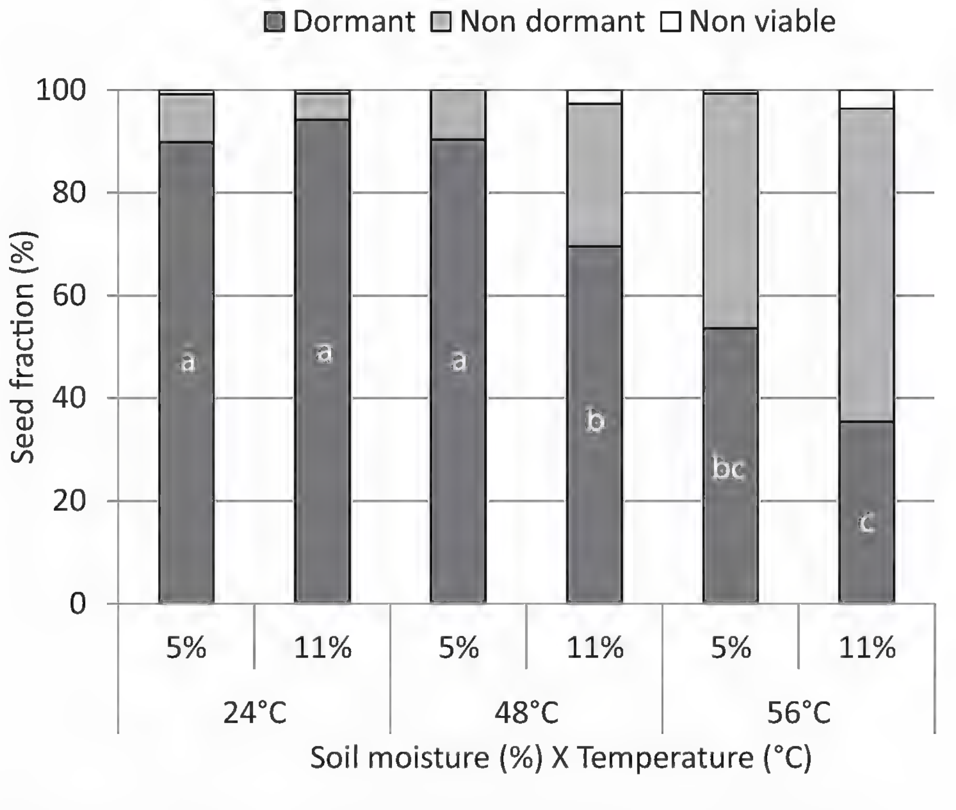

Figure 7. *Acacia saligna* seed response to various combinations of soil temperature and soil moisture under controlled conditions. Each combination included five replicates of 30 seeds.

Discussion

Effect of solarization on *A. saligna* seed viability and seedling emergence from the seed bank

Solarization was found to be highly effective in reducing the seed viability of both buried seeds and the seed bank of *A. saligna*. Solarization significantly increased the non-viable fraction of buried seeds compared to the control at all soil depths during the entire experimental duration, except for the 6–19 cm depth after 14 weeks. Exposing buried seeds to 14 weeks of solarization almost completely eliminated their viability throughout the upper 9 cm of the soil profile. It is interesting to note that although a large number of seeds in this treatment remained viable in the deeper soil layers, their root and shoot growth was very limited during the germination test. It is reasonable to assume that these "weakened seeds" would fail to emerge from the soil under natural conditions. Although there was an interaction between treatment, soil depth, and experimental duration, the viability rates at all soil depths and durations in the treated soil were significantly lower than those at respective depths and durations in untreated soil.

Solarization almost completely eliminated the viable seed fraction of the *A. saligna* seed bank. Consequently, seedling emergence was negligible in this treatment, in contrast to about 1,000 of emerging seedlings per square meter in the control. A small-scale solarization experiment (36 m^2 plot) was conducted during the following year (2016) in undisturbed soil (trees were cut and removed, but without bulldozer involvement) at a distance of 150 m from the site of the first main experiment (2015). A similar trend of reduction in both seed bank density and seedling emergence was observed.

Although solarization almost completely eliminated seedling emergence, a few small patches of densely germinating seeds were observed outside the sampled plots. We assume that these patches appeared in areas where the polyethylene sheet was punctured by sparks produced during prescribed burning, conducted adjacent to the experimental site. Sampling the soil in these patches showed that no seeds remained dormant in these sites (data not presented), indicating that the accumulated heat was sufficiently higher than the threshold of dormancy release, but not high enough for the loss of viability.

The underlying mechanism of seed bank reduction

The differences in maximum daily soil temperature and soil moisture recorded in the control and the solarization treatment were not large (48 and 56 °C and 5 and 11% moisture at 5 cm depth in the control and the solarization plots, respectively). However, our laboratory experiment demonstrated that these small differences in soil temperature and soil moisture profoundly affected the rate of release from seed dormancy. The interaction between these two main factors significantly affected the release from dormancy. At 56 °C and 11% moisture, the rate of release from dormancy was 60%, six-fold higher than at 48 °C and 5% moisture. Indeed, in the early stage of the field

experiment, i.e. 4 weeks after the onset of the solarization treatment, the non-dormant fraction was higher in the solarization treatment than in the control. As suggested in our previous studies (Cohen et al. 2008, 2018, 2019), we assume that the release from dormancy is probably the critical stage leading to the deterioration of the seed bank through a weakening effect occurring during soil solarization.

Is solarization a habitat-specific method?

As noted in the description of the study site, the habitat of the present study is characterized by relatively moist soil. Although our results show that the soil moisture in the bare soil was very low, the dominating presence of *P. farcta* and *G. glabra* in this site implies a high water table. There are data indicating that a high water table increases the soil moisture above it at a rate depending on the soil type (Miguez-Macho et al. 2008). In the present study, soil moisture increased significantly in the solarization treatment during the experimental period, probably due to condensation of water vapors under the polyethylene sheet, which rewetted the soil. This phenomenon could positively affect the efficacy of solarization. We assume that under non-optimal conditions for solarization, such as those prevailing in regions with a shorter or cooler summer or in a very dry soil, the solarization process might result in a lower seed mortality rate. In observations made in a dry soil with a deep water table, there was no change in seed viability, but an increase in the release from dormancy, which usually leads to high seedling emergence, was observed (unpublished data). Therefore, in such habitats, the release from dormancy alone might also be beneficial when integrated management that includes chemical control of the seedlings is recommended to complete the restoration process in the first winter following soil solarization.

Solarization is not a species-specific method

Solarization is not a species-specific method and might be applied to control the seed banks of a large spectrum of invasive plants. Our results show that solarization almost completely reduced the emergence of various species with physically dormant seeds, such as *Medicago polymorpha* L., *Geranium rotundifolium* L., and *Malva parviflora* L., which proliferated in the control plot. Moreover, solarization reduced the emergence of not only physically dormant seeds, but also of seeds with other types of dormancy mechanisms, including seeds with physiological dormancy (*Amaranthus albus* L., *Galium aparine* L., and *Glebionis coronarium* (L.) Tzvelev), seeds with combinational dormancy (physical and physiological) (*Geranium molle* L.), and seeds with morpho-physiological dormancy (*Parietaria lusitanica* L).

From a restoration perspective, soil solarization is a nonspecific disinfestation technique. If vegetation cover is planned to regenerate naturally, i.e. using passive management, the adverse effect of seed bank reduction by soil solarization must be considered.

However, the experience gained in restoration programs indicates that the reduction in density of the invasive plants caused by the control operation generally results in proliferation of other invasive plants (secondary invasion) or of local environmental weeds (D'Antonio and Meyerson 2002; Buckley et al. 2007; Le Maitre et al. 2011). In the current study, most of the plants that regenerated naturally in the control plots were local environmental weeds. In such cases, active revegetation using planting and/or seed sowing is essential for rehabilitation of the natural vegetation (Le Maitre et al. 2011). When active revegetation is planned, using soil solarization provides a significant advantage in preparing the area for targeted native species by reducing competition with undesirable plants.

Application and implications

Soil moisture is an essential component for the success of solarization (Shlevin et al. 2004; Cohen et al. 2008). Therefore, in dry habitats, the regular soil solarization method, which includes pre-irrigation, is recommended. Alternatively, satisfactory results can also be achieved by covering the soil with transparent polyethylene following the last rains (RBS method, Cohen et al. 2019). In wetlands, covering the soil during the summer without pre-irrigation (i.e., dry solarization, as used in this study) has also been found to be effective. The advantage of dry solarization over RBS is expressed by a shorter soil mulching duration, thus ensuring the intactness of the polyethylene sheet during the effective period of solarization. The current study demonstrates the versatility and efficacy of using this solarization approach in restoration programs in natural habitats.

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Supplementary material 1

Table S1. Effect of soil depth, treatment, experimental duration, and their interactions on soil moisture

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Data type: measurement

Explanation note: The data were analyzed by two-way ANOVA. Soil depth (SD): 0–5 and 15–20 cm; treatment (T): control and solarization; experimental duration (ED): 6, 28, 43, 51, and 66 days after mulching. n = four replicates of soil cores in each combination of soil depth and experimental duration. P values below 0.05 are marked in bold to indicate significant effects.

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Supplementary material 2

Tables S2, S3

Authors: Oded Cohen, Abraham Gamliel, Jaacov Katan, Iris Shubert, Aviv Guy, Gil Weber, Joseph Riov

Data type: measurement

Explanation note: **Table S2.** Effect of soil depth, treatment, experimental duration, and their interactions on the seed dynamics of *Acacia saligna*. The data were analyzed by three-way ANOVA. Soil depth (SD): 1–4, 6–9, 11–14, and 16–19 cm; treatment (T): solarization and control; experimental duration (ED): 4, 6, 11, and 14 weeks after mulching. The seed dynamics included dormant, non-dormant, and non-viable fractions. n = four replicates of buried seeds, 30 seeds in each. P values below 0.05 are marked in bold to indicate significant effects. **Table S3.** Post-hoc comparisons from the three-way ANOVA (Table S2). The main effects are treatment (T): control and solarization; soil depth (SD): 1–4, 6–9, 11–14, and 16–19 cm; and experimental duration (ED): 4, 6, 11, and 14 weeks after mulching. The seed dynamics included the following fractions: dormant (Table S3a), non-dormant (Table S3b), and non-viable (Table S3c). Values are means ± standard errors of eight replicates for each combination of treatment, soil depth, and experimental duration. Means with different letters are significantly different (t-test, $P < 0.05$ for treatment comparison; Tukey's-test $P < 0.05$ for all other comparisons).

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